



Integrating pattern with process at biogeographic boundaries: the legacy of Wallace

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Biogeography is a vital discipline today because of its extraordinarily integrative nature, drawing from and informing biological and Earth sciences in order to explain the history and future of life on our planet. Yet, even as we continue to build more sophisticated syntheses using molecular genetics, GIS-based distribution modelling, and ever-better analytical and visualizing approaches, we should recall that exploring causal connections between biological and Earth history is not a particularly new endeavor. For example, the biogeographic principles advocated in the late 1800s by Alfred Russel Wallace (see Box 2.1 in Lomolino et al. 2006) were infused with ideas associating distributional and diversification histories of organisms with geology and climate. But even a century before Wallace, in 1761 Comte de Buffon had recognized the differences between mammals in the New World and Old World tropics and proposed a rudimentary evolutionary causation for their divergence and distribution based on separation of formerly united continents.

Certainly, de Buffon and Wallace were not alone during their times in describing the non-random distributions of animals and plants, exploring causal explanations (see contributions reproduced in the “Early Classics” section of Lomolino et al. 2004), and recognizing regions of rapid transition between geographically distinct biotas. Wallace stood out, however, in the magnitude and synthetic nature of his focus on a single biogeographic boundary. After spending eight years exploring the mosaic of islands that lay between southeast Asia and New Guinea/Australia, Wallace concluded that “. . . we may consider it established that the Strait of Lombok (only 15 miles wide) marks the limits and abruptly separates two of the great zoological regions of the world” (Wallace 1860, pp. 173–174). He called this region the Malay Archipelago and it includes the most famous biogeographic transition of all, named Wallace’s Line by T. H. Huxley in 1868.

The four papers in this Special Feature were first presented in January 2009 in the “Patterns and Processes at Biogeographic Boundaries” symposium convened at the 4th Biennial Meeting of the International Biogeography

Society in Mérida, México. Here, we develop a background to these papers (Cody et al. 2010, Daza et al. 2010, Morrone 2010, Smith and Klicka 2010) by summarizing several highlights in the historical focus of biogeographers on boundaries.

Wallace’s Line: the iconic biogeographic boundary

Wallace was not satisfied with providing only a detailed description of the pattern of biotic transition across Wallace’s Line – he went on to speculate on the geological histories that underlay these differences: “I believe the western part to be a separated portion of continental Asia, the eastern the fragmentary prolongation of a former Pacific continent” (Wallace letter to Henry Bates in 1858 as reported by Berry 2002). At the same time that Wallace was delineating this geographically abrupt transition, he also was keenly aware that there were ongoing biogeographic processes that revealed a more complex situation: “The separation between these two regions [Sundaland and Wallacea] is not so absolute. There *is* some transition. There *are* species and genera common to the eastern and western islands” (Wallace 1860, p. 175). His grappling with these complexities reached its zenith when contemplating the history of the fauna on the island of Sulawesi (Celebes): “Its fauna presents the most puzzling relations, showing affinities to Java, to the Philippines, to the Moluccas, to New Guinea, to continental India, and even to Africa; so that it is almost impossible to decide whether to place it in the Oriental or the Australian region” (Wallace 1876 v. I, p. 389).

Beyond the more purely biogeographic observations of the patterns of biotic transition, Wallace took advantage of the wealth of biological diversity across islands within the Malay Archipelago to generate fundamental insights into the processes of evolutionary diversification and of speciation. In a paper now known as the Sarawak Law paper, he used an array of biogeographic and geological observations

to conclude that “Every species has come into existence coincident both in space and time with a pre-existing closely allied species” (Wallace 1855, p. 186). In the Ternate paper (Wallace 1858) he outlined the role of natural selection in the production of those new species. With these and a host of other papers, and with books including *The Malay Archipelago* in 1869 and *Island Life* in 1880, he firmly established the empirical importance of this biogeographic transition zone during the nascent years of the Darwinian revolution in biology.

Throughout the 20th century, evolutionary biologists and ecologists built upon the foundation that Wallace had established in the Malay Archipelago, with a good deal of concern for establishing the pattern of transition (e.g. the lines of Wallace, modified Wallace, Huxley, modified Huxley, Sclater, Weber [favored by Mayr 1944], Lydekker, etc.). Perhaps of most lasting influence, this biogeographic transition zone provided core evolutionary insights for Ernst Mayr (1942), and also played a major role in the formulation of new and often controversial models in evolutionary and ecological biogeography (Wilson 1959, Diamond 1974, 1975).

Beyond Wallace’s Line: the Nearctic – Neotropical transition zone

Wallace established three fundamental attributes of the Malay Archipelago that subsequently focused the attention of biogeographers on other biogeographic boundaries. The region marked an abrupt transition between long-isolated biotas, each of which represented hotspots of diversification and speciation, and complex patterns of interchange resulted as those once-isolated biotas collided. Wallace recognized similar attributes at the Mexican sub-Region of the Neotropical Region as it forms a boundary with the Nearctic Region. He used his vast compilations of both marine and terrestrial biotic affinities to postulate “it almost certain that the union of North and South America is comparatively a recent occurrence, and that during the Miocene and Pliocene periods, they were separated by a wide arm of the sea . . . [and that] when the evidence of both land and sea animals support each other as they do here, the conclusions arrived at are almost as certain as if we had (as we no doubt some day shall have) geological proof of these successive subsidences” (Wallace 1876 v. II, pp. 57–59).

Wallace relied on evidence from a relatively good mammalian fossil record to interpret biogeographic pattern and ecological consequences following the invasion of North American by a South American mammalian biota: “We have here unmistakable evidence of an extensive immigration from South into North America, not very long before the beginning of the Glacial epoch . . . How such large yet defenceless animals as tapirs and great terrestrial sloths, could have made their way into a country abounding in large felines equal in size and destructiveness to the lion and the tiger, with numerous wolves and bears of the largest size, is a great mystery . . . and the fact that no such migration had occurred for countless preceding ages, proves that some great barrier to the entrance of terrestrial mammalia which had previously existed, must for a time have been removed” (Wallace 1876 v. I, pp. 131–132).

In his reliance on mammals, Wallace initiated what developed throughout the 20th century into a dominant bias in the study of Late Cenozoic biogeographic and evolutionary dynamics between the Nearctic and Neotropical regions.

Other notable observations that emphasized the Pliocene interchange of mammals between North and South America included those of Karl A. von Zittel (1891) and Hermann von Ihering (1900). However, the modern stage was set by George Gaylord Simpson (1950), who famously sorted South American mammals into three temporally distinct faunas that he postulated to represent waves of immigration, most likely from North America: earliest Paleocene Ancient Immigrants (Oldtimers); Late Eocene to Miocene Island Hoppers; and late Tertiary to Recent Newcomers, the South American component of what now is known as the Great American Biotic Interchange (GABI).

Simpson (1950), like Wallace, was clearly interested in both the ecological and biogeographic attributes of northern and southern faunas that might explain the pattern of Neotropical and Nearctic interchange that he inferred: “Middle America is a faunal filter . . . Its ecological characteristics . . . determined which stocks were involved in faunal interchanges between North and South America and which are now immobilized to the north and to the south. The filtering action is not sharply localized. It begins well to the north (and west), roughly at the edge of the Lower Sonoran life zone in southwestern United States, and also reaches far to the south and east, more or less to the edge of the Guiana highlands and thence southward and westward” (Simpson 1950, p. 387).

Simpson’s attempt to delineate the geography and ecology of the transition zone between Nearctic and Neotropical biotas was continued into the latter 20th century primarily by entomologist Gonzalos Halffter: “I have defined as the Mexican Transition Zone . . . part of the southwestern United States, all of Mexico, and a large part of Central America extending to the Nicaraguan lowlands” (Halffter 1987, p. 95). Halffter’s Mexican Transition Zone has subsequently been refined through contributions including Ortega and Arita (1998) and many studies by Juan J. Morrone and his collaborators.

It became a hallmark of the GABI that modern mammal biotas in South America have a much higher percentage of taxa with northern ancestry than do biotas in North America with South American ancestry. Simpson surmised that mammals with northern ancestries were so successful in South America for two reasons. First, he considered them poised for a great invasion of South America following development of a land bridge because they had been adapting to tropical ecosystems in Central America, similar to those of northern South America, throughout the Cenozoic. Second, once in South America, the northern invaders were better competitors because of their long evolutionary history of being tested and surviving within the intense milieu of the World Continent: “When ecological vicars met, one or the other generally became extinct . . . Those [northern invaders] extant in the Plio-Pleistocene were the ones that had been successful in a long series of competitive episodes. They were specialists in invasion and in meeting competitive invaders” (Simpson 1950, pp. 382–383).

With his synthesis of biogeography, evolution, and ecology, Simpson laid the foundation for subsequent decades of investigations into the GABI led by the paleontologists S. David Webb and Larry G. Marshall. More information began to emerge on non-mammalian groups, and the “state-of-the-art” was summarized in a compendium edited by Stehli and Webb (1985), followed by updated data and models during the 1990s for mammals (Vrba 1992, Webb 2006), reptiles (Cadle and Greene 1993), and plants (Burnham and Graham 1999).

Integrating pattern with process at biogeographic boundaries

With this brief background, we are now in a position to ask: what properties of biogeographic boundaries continue to draw the focus of modern biogeographers? We suggest that minimally the following three advances are highly relevant to addressing this question, and are illustrated variously in the collection of studies presented in this Special Feature.

Advances in reconstructing Earth history

A geology infused by plate tectonics has brought into focus the dynamic relationship between plate boundaries and biogeographic boundaries. Many of the grandest biogeographic boundaries, including those discussed in detail here as well as the northward movements of India and Africa, represent collision boundaries between Gondwanan and Laurasian continental plates and adjacent oceanic plates, producing complex mosaics of island arcs, accreted terranes, mountain chains, and uplifted plateaus.

Wallace surely would have been satisfied in knowing how closely the first part of his speculation about the geological history of the Malay Archipelago region fit with modern reconstructions of Pleistocene cycles of connectivity and isolation of islands on the Sunda Shelf (Sundaland) with each other and with continental Asia (Voris 2000). However, he was not correct in postulating a former Pacific continent, and would have been astonished by the northward migration of the Australian plate during the Cenozoic Era, and the production of island arc volcanoes, accreted terranes, and minor plates along the leading edges of the Australian and Pacific oceanic plates (Wallacea) as they subduct under the Eurasian continental plate (Hall 2001, 2002). One can wonder how his puzzlement about the complex biota of Sulawesi would have changed had he known that this island represents the tectonic suturing of Gondwanan and Laurasian terranes during the Late Miocene (Hall 2001).

At the Nearctic–Neotropical boundary, Wallace’s prediction that great advances would allow geology to one day catch up to the strong biogeographic signal of recent suturing of North and South American biotas has been realized, although with some differences in details (Coates and Obando 1996, Iturralde-Vinent 2006, Kirby et al. 2008). Of great importance to biogeographers attempting to decipher the complexity of this biotic history are

emerging details about the timeframes and processes of landscape evolution, including the uplift of the northern Andes, the complex upland and lowland geological mosaic in Central America, development of the Trans-Mexican Volcanic Belt, uplift of the mountain ranges and plateaus in northern Mexico, and opening of the Gulf of California. The four papers in this volume illustrate how today’s studies of interactions within and across boundaries are being addressed within an interactive framework that can reciprocally inform biogeographic and geological reconstructions.

Advances in molecular biogeography and phylogeography

Modern studies of the biogeography of boundaries have been revolutionized with molecular genetics-based biogeography and phylogeography (Riddle et al. 2008) for several reasons. First, biogeographers can estimate phylogenetic and phylogeographic structure with great accuracy; often revealing a wealth of cryptic diversity in taxa within and across a boundary region. Second, biogeographers now have the capacity to address historical and ecological patterns in those taxa within a co-distributed biota that do not have a good fossil record. Third, many of today’s studies use properties of molecular evolution to estimate independently timeframes of isolation, interchange, and diversification.

The Malay Archipelago coincides closely with delineations identified variously as the Indo-Malay Archipelago, Indo-Malay-Philippine Archipelago, Indo-West Pacific, Indo-Australian Archipelago, Malesia, and Coral Triangle (Hoeksema 2007). Biogeographers are using molecular approaches to reveal patterns of diversity and processes of diversification within the Archipelago in both terrestrial (Heaney et al. 2005, van Welzen et al. 2005, Newbound et al. 2008, Uy et al. 2009) and marine (Barber et al. 2000, Briggs 2000, Lourie and Vincent 2004, Carpenter and Springer 2005, Hoeksema 2007, Williams and Duda 2008, Bellwood and Meyer 2009) taxa and biotas, providing critical information for biodiversity protection in one of the world’s great hotspots.

Turning again to questions of isolation, interchange, and diversification across the Nearctic–Neotropical transition zone, the contributions here by Smith and Klicka and by Cody et al. offer a complementary pair of analyses illustrating how biogeographers can use time-calibrated molecular phylogenies to begin to truly put the “Biotic” into the GABI, addressing the generality of the mammal-based patterns across a suite of non-mammalian taxa. Daza et al. also employ time-calibrated molecular phylogenies within a novel analytical approach to illustrate advances in our potential to address hypotheses of historical vicariance on the complex geographic tapestry of Middle America.

Advances in the integrative nature of biogeography

Finally, the contribution from Morrone synthesizes a number of studies that collectively have shed light on biogeographic pattern across the Mexican Transition Zone, the

core region of biotic reticulation between Nearctic and Neotropical elements. A fundamental contribution here lies in his synopsis of a step-wise, integrative approach that is an attempt to break through the log-jam of debate over approaches and concepts that has plagued historical biogeography for decades. Refreshingly, Morrone acknowledges that a multitude of legitimate questions reside within biogeography, and that different approaches are optimized to address different questions, but that an ultimate goal might be to assemble each into a series of analytical steps within a fully integrative research program (see also Riddle and Hafner 2006) that seeks to develop a geobiotic scenario for a given biogeographic system. One can, for example, view each of the other three contributions here as important contributions to, but not the entire story of, a fully realized geobiotic scenario for the Nearctic–Neotropical transition zone.

Biogeographic boundaries across Earth

Beyond the Malay Archipelago and Nearctic–Neotropical transition zone, biogeographers are actively exploring patterns and processes at a host of other biogeographic boundaries. For example, molecular-based studies are being combined with ecological, climatic, and fossil information to unravel the geobiotic scenarios of isolation, interchange and diversification between Palaearctic and Nearctic biotas across Beringia (Debruyne et al. 2008, DeChaine 2008, Elias and Crocker 2008, Haile et al. 2009); between the Indian subcontinent and Eurasia (Bossuyt and Milinkovitch 2001, Conti et al. 2002, Van Bocxlaer et al. 2006); and between Africa and Eurasia (Voelker 2002, Kodandaramaiah and Wahlberg 2007). We hope the papers in this Special Feature prove to be a valuable demonstration of several of the ways in which emerging approaches and concepts are allowing biogeographers to fully explore the fascinating patterns and processes at biogeographic boundaries that Alfred Russel Wallace could only begin to tap at the dawn of biogeography some 150 yr ago.

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